



**SVERIGES
LANTBRUKSUNIVERSITET**
Rapporter

**The influence of stand density and litter
quality on litter decomposition rates in
manipulated Scots pine forests.**

The effect of fertilization and irrigation.

**Björn Berg,
Carl Olof Tamm and
Aron Aronsson**

Institutionen för ekologi och miljövård
Swedish University of Agricultural Sciences
Department of Ecology and Environmental
Research

**Rapport 43
Report**

Uppsala 1991
ISSN 0348-422x
ISRN SLU-EKOMIL-R-43--SE

Tryck: SLU/Repro, Uppsala 1994

Abstract

Berg, B., Tamm, C.O., and Aronsson, A. 1991. The influence of stand density and litter quality on litter decomposition rates in manipulated Scots pine forests. The effect of fertilization and irrigation. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences. Report No 43. ISSN 0348-422x. ISRN SLU-EKOMIL-R-43--SE.

Litter decomposition was investigated in two experimental forests of Scots pine. Pine needle litter was thus incubated in plots that were either fertilized (F), irrigated (I) irrigated plus fertilized (IF) or control plots (C).

In the early stages of decomposition a higher mass-loss rate was observed in the F-plot, I-plot and IF-plot than in the C-plot. The higher concentration of nutrients in the litter from F-plot was too low to give any measurable effect on mass-loss rate in the early stages. On the other hand, green needles with extremely high nutrient concentration had a clearly higher initial decomposition rate than brown needle litter in both the C-plot and the IF-plot.

The higher rate was limited to the early stages only and during the later decomposition stages the mass-loss rates were very similar in all groups despite the conditions in the F-plot that promoted higher initial mass-loss rates.

During decomposition the concentration of lignin increased linearly as compared to litter mass loss. The concentration of lignin in the litter incubated in the F-plot and the I-plot increased faster than the concentration of lignin in the litter incubated in the C-plot. In the late stages of litter decomposition a clear difference was noted between the C-plot and the IF-plot. Annual mass loss of litter was compared to the lignin concentration at the beginning of the year. At the same lignin concentration the mass-loss rate still was higher in the IF-plot but the rate decreased markedly and much more quickly with increasing lignin concentrations than in the C-plot and the rates appeared either to converge or even to become inverted. One may speculate whether the conditions supporting a higher decomposition rate gave rise to a more recalcitrant humus.

Key words; Litter, decomposition, chemical composition, lignin, nutrients, Scots pine, fertilization.

Björn Berg¹, Carl Olof Tamm and Aron Aronsson Section of Production Ecology, Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, P.O. Box 7072, S-750 07 Uppsala, Sweden

1. Present address: Department of Forest Soils, Swedish University of Agricultural Sciences, P.O. Box 7001, S-750 07 Uppsala

Contents

Abstract	3
Introduction	5
Site descriptions	6
Site Norrliden	6
Site Jädraås	6
Control plot	6
Fertilized plot (solid fertilizer)	6
Irrigated plot	6
Irrigated plus fertilized plot	7
Material and methods	7
Needle litter collection	7
Site Jädraås	7
Site Norrliden	7
A study on needles ageing on trees and forming needle litter	7
Storage and sample preparation of litter for decomposition experiments	7
Decomposition experiments	7
Site Jädraås	7
Site Norrliden	8
Sampling and mass-loss determination	8
Chemical analyses	8
Basic data	8
Results and discussion	8
Terminology	8
Initial chemical composition of nitrogen of the litters	8
Plot averages Jädraås	8
Plot averages Norrliden	9
Formation of needle litter on some single trees	9
Litter decomposition patterns in plots given different treatments	11
Factors which affect litter mass-loss rate	11
Climatic factors and variation among plots given different treatments	11
The effect of the litter's chemical composition on mass-loss rate in early decomposition stages	12
The effect of lignin concentration on mass-loss rate in later decomposition stages	12
Comparison of mass-loss between brown and green needle litter	15
Concluding remarks	15
References	18
Tables	20
Appendix 1	22
Appendix 2	23

Introduction

In coniferous forests it has been suggested that acid soils and nutrient-poor, lignin-rich litter contribute to the slow decomposition of coniferous litter. In undisturbed forest sites of the boreal zone this leads to an accumulation of organic matter on the forest floor, immobilization of essential nutrients, especially nitrogen, thereby eventually reducing tree growth (Hesselman 1937; Sirén 1955; Tamm and Carbonnier 1961). In northern Scandinavia forestry practices have been designed to overcome the inconveniences of these situations by reducing and activating the existing forest floor. It is clear that in both cases there is a need for basic knowledge about the decomposition process of organic matter and its rôle in tree nutrition.

The litter-decomposing microorganisms are dependent on temperature and moisture for their activity, which determines the decomposition rate of litter. Several studies - especially in the laboratory - have been made to correlate the microbial activity measured as CO₂ release or O₂ consumption, to temperature and moisture in, e.g., soil cores. In a field study on litter decomposition Jansson and Berg (1985) could explain as much as 95 per cent of the decomposition rate of newly shed Scots pine needle litter.

Of other factors that influence the turn-over rate of the forest floor, the chemical composition of the added litter has received some attention. In a number of studies the nitrogen concentration of the substrate was concluded to be a rate-limiting factor for litter decomposition (Melin 1930; Kelly and Henderson 1978; Edmonds 1980). In view of the frequent use of nitrogen fertilizer in North-Swedish forests (Holmen 1983) this has a silvicultural interest, since fertilized trees produce a litter with a very different nutrient composition as compared to non-fertilized forests (Miller and Miller 1976; Berg and Staaf 1980b).

Part of the concept "litter quality" includes e.g. initial concentrations of phosphorus and calcium (Van Cleve 1974), lignin (Fogel and Cromack 1977; Meentemeyer 1978), soluble organic matter (Berg and Lundmark 1987), as proposed indices for rate regulation. Of these variables decomposition is often

positively related to the concentrations of nitrogen, phosphorus, base minerals, and soluble organic compounds but negatively to levels of lignin and of tannins.

In a study on decomposition of Scots pine needle litter in central Sweden, Berg and Staaf (1980b) found that the strong positive relation of mass-loss to the nitrogen and phosphorus concentrations during the initial stages mass-loss disappeared as the decomposition proceeded. It was suggested that lignin, which progressively was accumulated in the litter, gradually became the most influential substance on mass-loss rate. A similar development was reported by Pandey and Singh (1982) in a study on decomposing deciduous and coniferous tree litter in the Himalayas. They noted that as decomposition proceeded, the relation between mass-loss rate and concentrations of nitrogen, calcium and water-soluble substances in the substrates weakened and that to lignin became stronger. Other examples of how initial differences in decomposition rates, related to litter type, levelled out or became reversed in later stages of decay, are given by Edmonds (1980), Berg *et al.* (1982a); Berg (1984), and Berg and Ekbohm (1991).

In the present study we have investigated the decomposition rates and patterns of Scots pine needle litter in stands given solid nitrogen, phosphorus and potassium fertilizer as well as ones that were irrigated only or irrigated plus fertilized with dissolved fertilizer.

Site descriptions

Site Norrliden

The site Norrliden is located about 100 km north-west of Umeå in northern Sweden (64°21'N; 19°46'E) at an altitude of 260 m. The annual mean temperature is +1.3 °C and the annual precipitation 680 mm (Vedin, 1973). Average actual evapotranspiration (AET) is 360 mm and the length of growing season 145 days, as calculated on the basis of a

5 °C limit. The soil type is a till with a well developed iron podzol. The area, clearcut in 1951, was burnt the following year and planted in 1953 with Scots pine (*Pinus sylvestris* L.) (Tamm *et al.* 1974).

The plantation, which is an optimum nutrition experiment with Scots pine in monoculture, started in 1953. The area is divided into plots (40 m x 40 m) given different fertilizer regimes (Tamm *et al.* 1974). In our experiment we selected four of these, namely control (N0), low nitrogen, high phosphorus (N1P2), high nitrogen, high phosphorus (N2P2) and high phosphorus (P2). The exact dosages are given in Appendix 1.

Site Jädraås

The 20-30 year old Scots pine stand studied is located at the SWECON research site, Ivantjårsheden, central Sweden (60°49'N; 16°30'E) at an altitude of 185 m, on a flat area of deep glacial sand sediments. The mean annual precipitation at a nearby village is 609 mm (1931-60), and the mean annual temperature +3.8°C. The length of the growing season is about 160 days (number of days with a daily temperature higher than 6°C; Axelsson and Bråkenhielm 1980). The tree layer is exclusively composed of Scots pine and had a height of 6-7 m in 1986.

The pH-range is 3.9-4.2 in the humus layer and 4.6-4.8 in the upper mineral soil. The parent mineral material as well as the whole soil is very poor in essential nutrients. The C-to-N ratio of the A₀₁ - A₀₂ layer is in the range 40-45.

The stand is divided into experimental plots of four kinds, namely control (C), fertilized plot (F), irrigated plot (I) and an irrigated and fertilized plot (IF).

Control plot

Heather (*Calluna vulgaris*) and cowberry (*Vaccinium vitis-idaea*) form a well-developed field layer, and the bottom layer completely covering the ground, is mainly composed of the mosses *Pleurozium schreberi* and *Dicranum polysetum* Sv together with *Cladonia* lichens. The most recent direct effect of forestry practices was a thinning in 1973. A more complete description is given by Axelsson and Bråkenhielm

(1980). A very loose litter layer (A₀₀), interwoven with living mosses and lichens, covers a humus layer (A₀₁-A₀₂) of about 2.2 cm thickness. The soil profile is an iron podsol with a weakly developed bleached horizon (2-7 cm) and the humus type is a typical mor. The A₀₁ (F) and A₀₂ (H) horizons are almost indistinguishable from each other.

Fertilized plot (solid fertilizer).

Since 1974 this plot has been fertilized with 80 kg ha⁻¹ yr⁻¹ of nitrogen and from 1981 the amount was 50 kg ha⁻¹ yr⁻¹ of nitrogen. The amounts of added phosphorus and potassium have been 30 kg ha⁻¹ and 60 kg ha⁻¹ every third year respectively (cf. Appendix 2). The canopy cover has become much denser as compared to the control plots and there was practically no ground vegetation; but the soil is covered with a layer of needle litter. The humus layer had increased in thickness to 2.7 cm as compared to the control whereas the bleached soil was unaffected.

Irrigated plot

Since 1974 this plot has been irrigated with between 100 and 300 mm in the summer periods (end of May to mid September) in order to reach a total (natural rain plus irrigation) rainfall of around 500 mm in that period, which is about double the rainfall or about 4.5 mm day⁻¹ (Appendix 2). The most marked effect was a heavy growth of the moss layer, which increased from being almost nonexistent in the control to a plot-covering layer about 11 cm thick. Also the heather increased in amount, whereas the lichens disappeared completely. The pines showed an increased growth but the canopy cover was mainly unaffected. The humus layer had the same thickness as that of the control and the bleached soil was unaffected.

Irrigated plus fertilized plot.

Since 1974 this plot has been given a balanced solution of nutrients (Ingestad 1967), in the irrigation water, the irrigation scheme being the same as for the irrigated plots (cf. Appendix 2 and above). The most evident changes are the very dense canopy cover and the rich herb layer of fireweed (*Chamaenerion angustifolium*) and raspberry (*Rubus idaeus*) which have produced a thick cover about 1 m tall. The soil type has changed and the humus layer had clearly increased in thickness to 2.9 cm. No difference to the control plot was seen in the bleached soil.

Materials and methods

Needle litter collection.

Site Jädraås

Needle litter was collected in two experimental areas. Sampling of unfertilized needle litter (unified needle litter) from the branches of trees in a Scots pine stand, aged about 15 years, took place at Ivan-tjärnsheden (Jädraås) in the autumns of 1981 until 1986. Brown needles from the falling needle generation were taken at abscission from trees growing in an area of about 50 m x 50 m. The chemical variation between years of needle litter from the Jädraås plot has been described by Staaf and Berg (1989) and by Berg (1982). This type of litter was used in the decomposition experiments as a unified litter among the different plots.

Green, nutrient-rich needle litters were collected at the same plot at winter as two- and three-year old needles. After sampling they were treated like the unified litter.

Needle litters from the plots given different treatments (plot-specific needle litter) were sampled as described above in late September of 1982, 1983 and 1984. Samplings were made in the treated plots from at least ten trees per plot. In the 1982 sampling litter was collected from only one plot per treatment, whereas in the two years following, samplings were made in four plots per treatment.

Site Norrliden

Local litter from the Norrliden site was collected from the control plot and from plots heavily fertilized with N and P (N2P2, N1P2, and P2; cf. Appendix 1) and sampled from at least 10 trees within the plot.

A study on needles ageing on trees and forming needle litter

In one plot of each treatment one tree was selected, and from one branch needles of the fourth year class were collected. These samplings, made in 1976 and in 1977, were made on 6 occasions in 1976 and on 7 occasions in 1977. All samplings were made in the period from early August until mid-October.

Storage and sample preparation of litter for decomposition experiments.

Before weighing, the needle litter was air-dried at room temperature to about 5-8 per cent moisture. Dry mass was determined at 85°C and the largest difference in moisture was less than 0.5 per cent units of the average ($n=25$). Litter-bags were incubated in the different plots as described by Berg and Staaf (1980a).

Decomposition experiments

Site Jädraås

To register differences in decomposition rates between treatments as dependent on soil climate, litter-bags with unified needle litter were incubated three times a year, namely in late May, early September, and late October each year. In the plots given different treatments (C,F,I and IF), bags with the plot's own litter were incubated together with bags containing unified needle litter. Further, permutations were made using local litter and in the control plots needle litters from all treatments were incubated as well as green needle litter.

Site Norrliden

To register differences in decomposition rates between treatments as dependent on soil climate, litter-bags with unified needle litter were incubated three times a year, namely in late May, early September, and late October each year. In the plots given different treatments bags with the plot's own litter were incubated together with bags containing unified needle litter. Further, permutations were made using local litter and in the control plots needle litters from all treatments were incubated as well as green needle litter. Litter-bags were incubated in the 36-year-old Scots pine plots as described by Berg and Staaf (1980a). Samplings were made three times annually. Four plots were selected for the incubations, namely a control plot, an N2P2 plot, an N2P1 plot and a P2 plot. At each of these, unified litter was incubated as well as green needle litter and local litter.

Sampling and mass-loss determination.

At each sampling one litter bag from each incubation set of each of the 25 incubation spots was collected. The litter bags were transported directly to the laboratory and cleaned of moss, lichen and dwarf shrub remnants. After drying at 85°C they were weighed individually and then each set of 25 bags was pooled to one sample before the chemical analyses were carried out.

Chemical analyses

Samples were ground in a laboratory mill equipped with a 1 mm screen. The amounts of water-soluble substances were determined by ultrasonic treatment of the milled sample three times in an ultrasonic bath and by weighing the samples after filtration and drying. The analysis for sulfuric-acid lignin was carried out according to Bethge *et al.* (1971) (see also Berg *et al.* 1982b). Nitrogen was determined by a micro-Kjeldahl method using a flow injection analysis apparatus (Bifok FIA 05, Tecator, Höganäs, Sweden) with gas diffusion and using phenol red as indicator (Svensson and Anfält 1982). For analysis of phosphorus, sulfur, magnesium, calcium, potassium and manganese, samples were digested for 2 days in a 2.5:1 (v/v) solution of nitric and perchloric acid. The analyses were performed by plasma atomic emission spectrometry (ICP-AES; Instrumentation Laboratory IL P-200, Andover, Massachusetts, USA).

Basic data

All data on litter mass loss and the chemical analyses are stored on computer for detailed analysis and are, in addition, available in a report (Berg *et al.* 1986; 1991).

Results and discussion

Terminology

We have used the term "lignin" for sulfuric-acid lignin throughout the paper but are aware of that the

term is not fully correct as the analytical method used also could include other compounds formed during the decomposition process, e.g. humification products and chitin (Berg and Theander 1984). In a study on decomposing litter, Nordén and Berg (1989) showed that there was a very high linear correlation between sulfuric-acid lignin and lignin as determined by high resolution ¹³C-NMR. The latter method also indicated that there was no measurable qualitative difference between aromatic responses in fresh and far-decomposed samples.

In the following we have used abbreviations for the different plot treatments. For the Jädraås site; C for control, I for irrigated plots, F for fertilized plots and IF for plots with fertilization plus irrigation (fertilizer dissolved in the irrigation water). For the Norrleden site; C for control, N3, N2, N2P2 and N1P2 for the heavily fertilized plots and N1 for a plot given a lower dosage of nitrogen (cf. Appendix No 1).

Initial chemical composition of the litters

Plot averages Jädraås.

Five investigations, each on a separate year, were made on the chemical composition of litter. In two of these (and in 1977), only nitrogen concentrations were investigated whereas in the three later ones (in the years 1982, 1983, 1984), analyses were made also on water solubles, ethanol solubles and lignin (Table 1). The concentrations of nitrogen were clearly affected by the treatments and it appears that litter from the trees of the F-plot and the IF-plots had concentrations (0.42 and 0.44 per cent) which were significantly higher than those from the C- and I-plots (0.36 per cent; Table 1). Over the five-year period there was no significant difference between C- and I-plot needle litters. Even though there was a variation in nitrogen concentrations in needle litter between the different treatments, which was statistically significant (C and I vs F; C and I vs IF), and which may last, it is worth noting that these differences were well within the variation observed by Berg (1986) and Staaf and Berg (1989). There were no significant differences in water-soluble substances among treatments when the average values were compared.

Variation between the years was considerable, with 21 and 10 per cent as extreme values in the C-plot and similar variations within the other plots. The average values might hint, though, that there could be a difference between I-plots and those not irrigated, the irrigated ones having average values around 11.5 per cent and the C- and F-plot litters having concentrations of 17.8 and 14.6 respectively. For the ethanol-soluble substances no great variation was seen, the average values being very close to and around 10 to 11 per cent.

It appears that the two plots that had been irrigated had litter with higher lignin concentrations than the two drier ones. On the other hand, this difference was very small and not statistically significant (Table 1; B. Berg and A. Aronsson, unpublished).

Plot averages Norrliden

Systematic samplings of needle litter were carried out on the different types of plots (Table 2) and some chemical components were investigated. No major differences were seen between treatments as regards water-solubles, ethanol solubles and lignin, the latter component being about 26 per cent. There appears, however, to be a small difference between years as regards the water-soluble fractions, which were small in the 1984 sampling.

The nitrogen concentration was considerably higher in the needle litter from fertilized plots, N3 needles having an average concentration of 0.83 per cent as compared to 0.38 per cent for control litter plot. This kind of observation has been made earlier (Berg and Staaf, 1980b; Berg 1986). Needle litter from limed plots had the same level as that from the control plots (0.38 per cent). There was no difference between the control, the N3 plot and the limed plot as regards the concentrations of phosphorus in the needle litter, the general level being 0.225-0.260 mg g⁻¹.

In an earlier study, Berg and Staaf (1980a) had found a positive linear relation between nitrogen and lignin concentrations in Scots pine needle litter. This was also found for Norway spruce needle litter (B. Berg, unpubl.). It appeared, though, that this may be

an indirect effect of the nitrogen fertilization. With the increased growth rates, the available boron was insufficient, as is clearly seen on the trees (Aronsson, 1985). The lowered boron levels also caused an increased lignin synthesis, through a disturbance of an enzymatic system (cf. Dugger, 1983).

Formation of needle litter on some single trees.

In a special study made at the Jädraås site, the needle generation to be shed was followed from early August until late October (Figure 1). We may see that the two plots given fertilizer (F- and IF-plots) had needles with relatively high concentrations of nitrogen still in the first week in August (1.2 - 1.3 per cent), whereas needles on trees in C-plots had levels around 0.8 per cent. It is noteworthy that the difference between the treatments was relatively smaller when the needles were finally shed, even though the order among them was retained. The needle litter from fertilized (F and IF) trees for both years was above 0.4 per cent, whereas those from C- and I-plot trees varied between 0.34 and 0.38 per cent.

Litter decomposition patterns in plots given different treatments.

With the selected sites and substrate, the decomposition process in the control plots should be almost completely microbial (Persson *et al.* 1980), since the influence by soil animals has been found to be quantitatively insignificant (Berg *et al.* 1980). Needle litter also has a very low leachability (< 1 per cent of the mass could be leached initially).

As decomposition proceeded the easily decomposable compounds disappeared first and the more recalcitrant lignin was left and thus accumulated (Berg *et al.* 1982b). It is seen that the concentration of lignin increased almost linearly with accumulated mass loss, both in the fertilized plot and in the control plot (Norrliden site). There was a clear difference, though, between the two plots. The concentration of lignin increased relatively faster in the fertilized plot.

It was possible to see a difference between the plots also at the Jädraås site. The increases in lignin

Nitrogen conc.
(%)

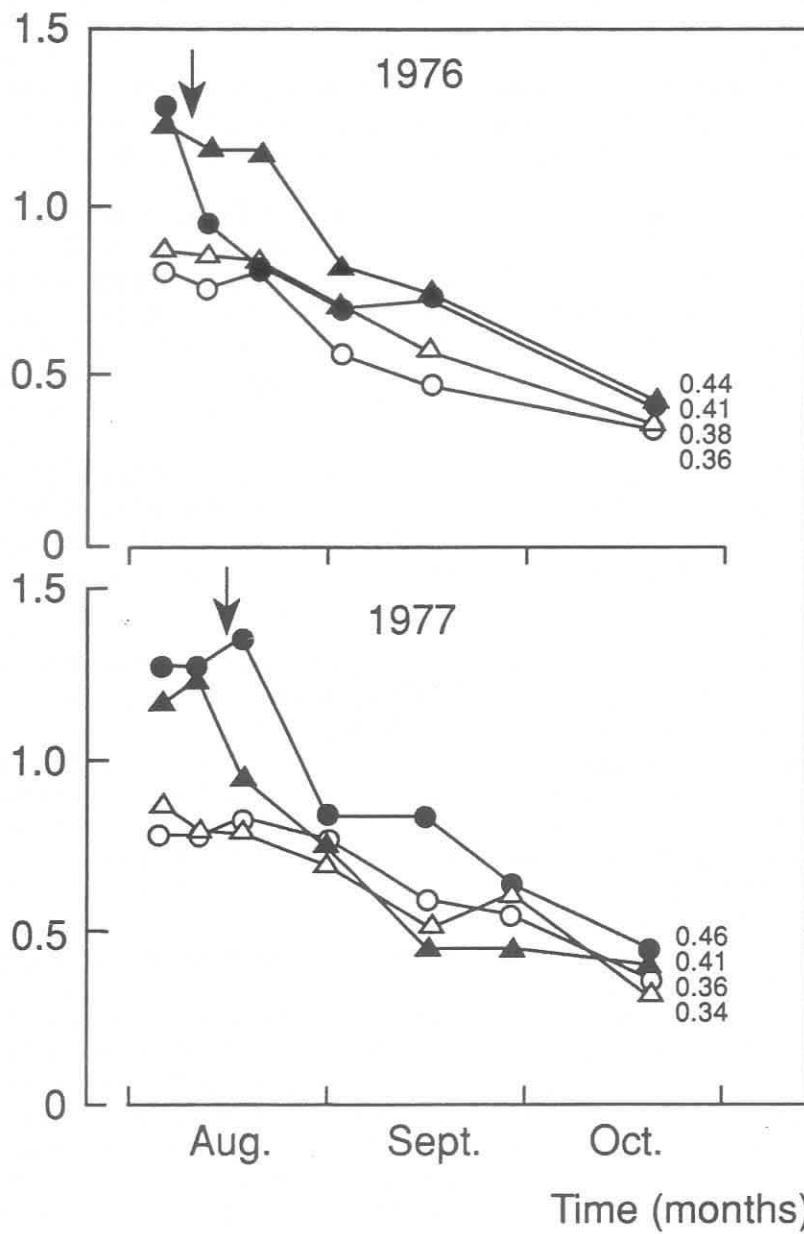


Figure 1. Nitrogen concentrations in needles to be shed at the end of the growing season in the years of 1976 and 1977. Sampling made from needles becoming yellow. (○) control plot; (△) irrigated plot; (●) fertilized plot; (▲) irrigated and fertilized plot.

concentration vs. accumulated mass loss for the C-plot and the I-plot had the same slope and followed the same graph. In both the F-plot and the IF-plot the concentration of lignin increased relatively faster. Such an observation was also made in a study on decomposition of Norway spruce needle litter in a fertilization experiment (Berg and Tamm, 1991a,b). In that study, the increases in lignin concentration were considerably faster for Norway spruce needle litters incubated in a plot heavily fertilized with nitrogen plus phosphorus, and the lignin concentration increased at about twice the rate as compared to the increase in litter incubated in the control plot. A similar observation was made for Scots pine needle litter in a climatic transect. From the observation in the climatic transect (Berg *et al.* 1990), the faster is the mass-loss rate of litter, the faster are increases in lignin concentration as compared to accumulated mass loss.

Factors which affect litter mass-loss rate.

Climatic factors and variation among plots given different treatments.

There was a difference in annual mass-loss rates in the C-plot at the Jädraås site (Table 3). Such a between-year variation at a nearby site has been described by Jansson and Berg (1985). They found that soil-water activity was the dominating rate-regulating factor at that site - situated 500 m from the plot of the present investigation and on the same type of soil. That a higher supply of water increased mass-loss rate is seen from the decomposition values of the irrigated I-plot, which were higher than those of the C-plot for all 1-year periods studied (Table 3). An example is the first year with measurements (Nov.-82 - Nov. -83), when the litter incubated in the C-plot had a mass loss of 21.6 per cent and that incubated in the I-plot, 34.2 per cent. The mean values of seven incubations were 26.7 and 30.6 respectively. Fertilization plus irrigation increased the first-year mass loss even further, and the average value from three incubations was 42.8 per cent. Also fertilization with solid fertilizer gave directly or indirectly a higher first-year mass loss, and the average value of six incubations was 28.6 per cent, although this value was not significantly different from those of the C- and I-plots.

The mean values (Table 3) gave a clear tendency in mass-loss rates for litter in early stages of decomposition. When comparing the average mass-loss rate in the IF-plot to that of the C-plot, we may note that in the former plot the rate was 60 per cent higher (difference statistically significant) whereas for the plot that was irrigated (I-plot) it was 15 per cent higher (significantly different). On the other hand, a comparison based on average values revealed that the difference between the C-plot and the F-plot was not significant.

The soil climate is affected by canopy cover, the character of the understorey and thickness of the organic soil layer (P.-E. Jansson, pers. comm.), and these plot properties vary between the treatments. It is not yet possible to distinguish all the separate effects, even though the sum of them was clearly measurable.

At the Norrliden site there appeared to be differences in mass-loss rate as influenced by ground climate between the C-plot and the N2P2-plot. It thus appeared that the average first-year mass loss of unified litter was 26.5 per cent in the C plot and in the N2P2-plot, 30.6 per cent. In the N2P-plot the average mass-loss value was 29.5 per cent. In both fertilized plots the litter mass loss was significantly higher than in the control plot (Table 4). We may see, however, when considering the variation between separate periods (Table 4), that the variation between years for one site was great enough to cause an overlap of mass-loss values.

The effect of the litter's chemical composition on mass-loss rate in early decomposition stages.

Litter decomposition rates were regulated not only by ground climate (above) but are also strongly influenced by the chemical composition of the litter (Berg and Staaf 1980b). However, it was found in the present investigation that the variation in chemical composition between the litters caused by these kinds of treatment was too small to give any significant effect on decomposition rates. Thus it was seen that in the C-plot (Jädraås site), litter mass-loss rates in the first year were not regulated by concentrations of nitrogen and phosphorus. Similar results were obtained from the IF-plot. We may

thus conclude that the effect of raised nutrient levels due to fertilization in the present case was too small to be registered as significant by the method used.

When the nutrient-rich green needles are included, the clearly higher mass-loss rate measured (caused by both nitrogen and phosphorus concentrations) affected the relation between mass-loss rate and nutrient concentration.

The effect of lignin concentration on mass-loss rate in later decomposition stages.

Lignin concentrations have been found to affect litter decomposition rates strongly (Berg and Staaf 1980; McClaugherty and Berg 1987) viz. high lignin concentrations have a rate-retarding effect. In later stages (>20 per cent accumulated litter mass loss), when lignin concentrations increased enough to retard litter mass-loss rate (McClaugherty and Berg 1987; Berg and Staaf 1980b), decomposition rates decreased in all treatments at both sites (basic data from Berg *et al.* 1991).

This observation was made at the experimental site Norrliden (Figure 2a) and the relation was highly significant ($r=-0.827$; $n=21$; $p<0.001$). It is noteworthy that the measurements from the control plot and those from the fertilized plot fitted well on the same line. It is thus possible that application of solid fertilizer in this case had little direct or indirect effect on decomposition rates in late stages. At least it was not possible to distinguish any difference. In the I-plot at the Jädraås site the effect of irrigation on litter decomposition rate in late stages was noteworthy. The mass-loss rate, as compared to concentration of lignin, was higher than in the C-plot (Figure 2b). A very similar phenomenon was reported by Berg *et al.* (1990) from decomposition studies in a 3000 km long climatic transect. In the southern sites, at which a higher initial mass-loss rate was promoted by a warmer and wetter climate, the effect of lignin on mass-loss rate was stronger than in the northern sites which were colder and drier.

Lignin decomposition is a slow process and some studies indicate that the decomposition rates of lignin and consequently also of litter in the late stages

of decomposition are regulated so strongly by the substrate that the climatic influence would be much less pronounced than in the early stages (cf. Berg and Ågren 1984; McClaugherty and Berg 1987). Mass-loss values for the C- and the IF-plots (Jädraås site) were plotted *versus* concentrations of lignin. In both cases highly significant linear relations were obtained with $r=-0.649$; $n=22$; $p<0.001$ (C-plot) and $r=-0.972$; $n=6$; $p<0.01$ for the IF-plot. The latter regression line had, however, a considerably steeper slope and a higher intercept than that of the C-plot litter (Figure 2b). The value pairs for the F- and I-plots are indicated (Figure 2b), but in no case was there a significant relationship. We may note that the two regression lines converged and one may expect that at some point above a concentration of 500 mg g^{-1} of lignin they will meet or cross each other. Even if the litter in the IF-plot thus had a higher mass-loss rate it was also more strongly affected by the increasing lignin concentration. One may speculate whether this will mean a more recalcitrant humus in the IF-plot as compared to the C-plot. An observation worth mentioning was that made by Söderström *et al.* (1983). When measuring soil respiration from a set of nitrogen-fertilized plots, they found a negative and significant effect of nitrogen additions on humus respiration as well as on live bacterial biomasses (direct counts).

The effect of an annual addition of solid fertilizer using the dosages of the present study, could not be seen to affect the litter decomposition rate in late decomposition phases. The measurement points did not deviate in any way from those of the control plot neither at the Norrliden site nor at the Jädraås site. This was also noted in two other studies (Berg and Tamm, 1991a,b) for Norway spruce. The effect on mass-loss rate in late stages, caused by irrigation, seemed clear, with the measured values well above the C-plot regression line (Figure 2b), although the number of measurement points was too low to indicate any relationship.

Comparison of mass-loss between brown and green needle litter.

In an earlier study (Berg *et al.* 1982a) it was seen that although nutrient-rich green needles initially were decomposed at a relatively high rate they later

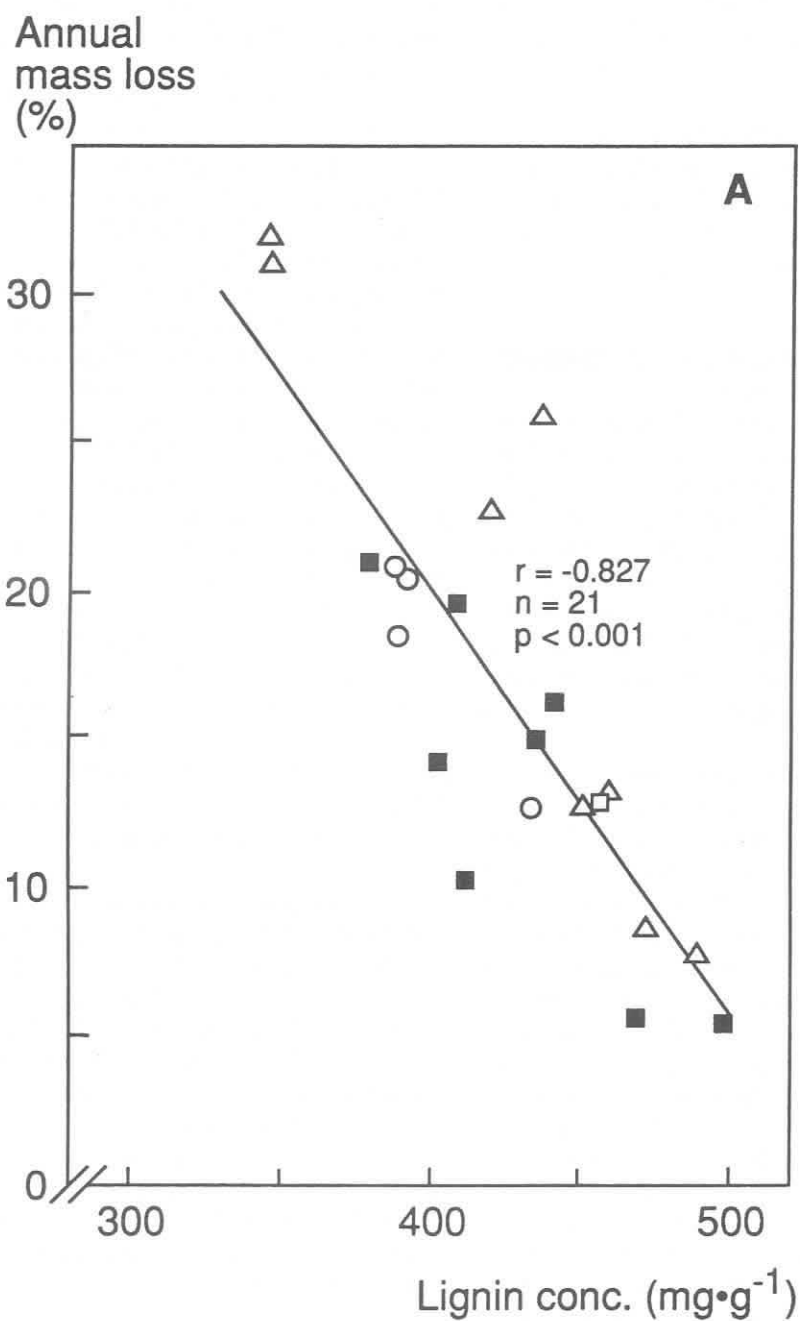
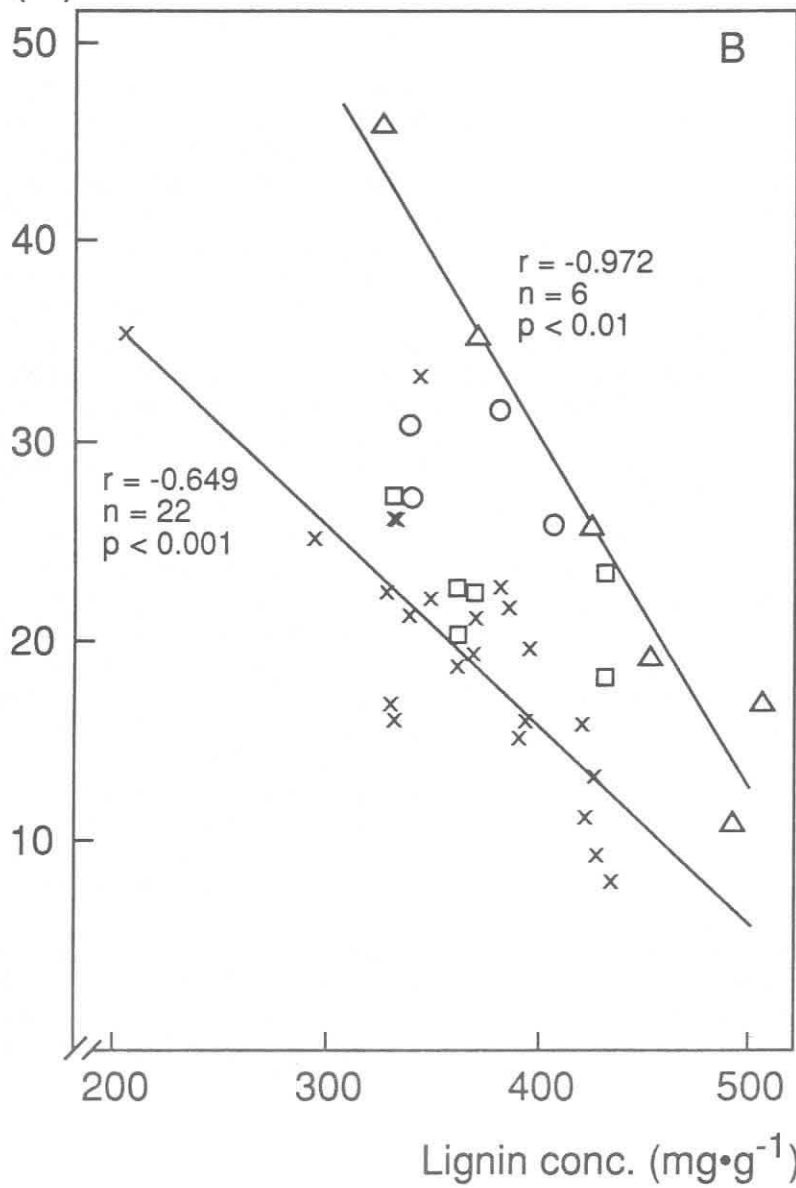


Figure 2. Linear relations between annual mass loss of litter plotted versus its concentration of lignin at the start of each one-year period. A. The Norrliden site; (○) control plot (□) fertilized plot (△) green needle litter in both plots.

Annual
mass loss
(%)



B. The Jädraås site; Litter in control plot (x), irrigated plot (o), fertilized plot (□) and irrigated plus fertilized plot (Δ). The lower line was drawn using control-plot data and the upper one with IF-plot data from the irrigated + fertilized plot.

were decomposed at a much lower rate than the more nutrient-poor brown needle litter. After three years' decomposition the accumulated mass loss for the brown needles was actually higher than that of the green ones, which had almost stopped losing mass. The same phenomenon was generalised in a later study (Berg and Ekbohm, 1991) where grey alder and white birch leaves as well as green and brown needles from Scots pine and lodgepole pine were found to behave likewise.

In the present study the former experiment was repeated in the C-plot and the IF-plot (Figure 3). The earlier observed phenomenon was less pronounced, but it could still be clearly seen that even if the green needles were decomposed at a high rate initially, both litter types had the same accumulated mass loss (55-60 per cent) after four years. In the IF-plot both litter types were decomposed considerably faster in the first year and the green needles by as much as 55 per cent, as compared to 32 per cent for green needles in the C-plot.

After about three years the difference in accumulated mass loss between the plots was considerably smaller. In the C-plot the accumulated mass-loss was about 50 per cent and in the IF-plot about 55 per cent. The experiment had to be interrupted in the latter plot simply because of fragmentation of the needles. For the green ones it was not possible to follow decomposition for longer than about two years, and for the brown ones, three years.

Concluding remarks.

In the early stages of decomposition a higher mass-loss rate was observed in all plots to which fertilizer had been added, as compared to the control plot. This higher rate was limited to the early stages only, and at later decomposition stages the mass-loss rates were very similar in all plots, in spite of the

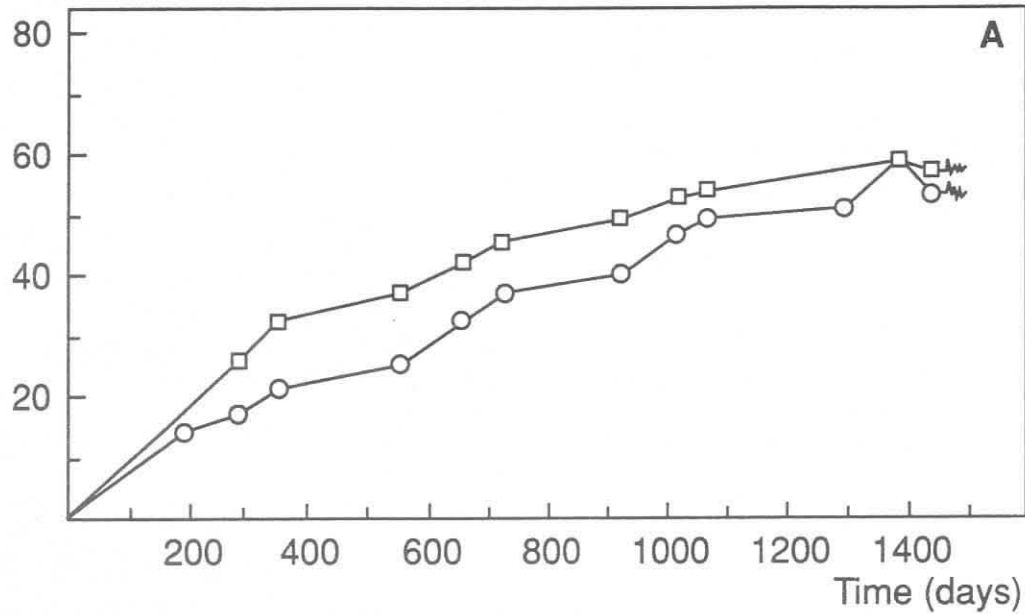
conditions in the fertilized plots that promoted higher initial mass-loss rates.

The higher concentration of nutrients in the litter from fertilized plots was too low to give any measurable effect on mass-loss rate in the early stages. On the other hand, green needles with an extremely high nutrient concentration had a clearly higher initial decomposition rate than brown needle litter in both the C-plot and the IF-plot.

In the late stages of litter decomposition, a clear difference was noted between the C-plot and the IF-plot. At the same lignin concentration the mass-loss rate was higher in the IF-plot, but the rate decreased markedly and much more quickly with increasing lignin concentrations than in the control plot. We may speculate that the rates may converge or even become inverted. One may also speculate whether the conditions supporting a higher decomposition rate gave rise to a more recalcitrant humus. Similar phenomena which support such a conclusion have been seen in other contexts (e.g. Berg and Ekbohm 1991; Söderström *et al.* 1983). In this stand the biomass production on the IF-plot was considerably higher than on the C-plot. The fact that a thicker organic layer has developed may, of course, partly be an effect of a higher litter production. We have seen, however, that the initial, relatively large difference in mass-loss rate between plots decreased as the litter became more degraded. We have also seen that in later stages a main rate-regulating component, namely lignin, had a gradually increasing, rate-hampering effect on mass-loss rate that was greater in the IF-plot than in the C-plot, and it even seemed possible that in very late stages the rate of mass loss in this case could be lower.

We may thus conclude that the increased thickness of the humus layer depends not only on a higher production of litter but apparently also on a quickly decreasing mass-loss rate as the litter decomposes.

Accumulated
mass loss
(%)



Accumulated
mass loss
(%)

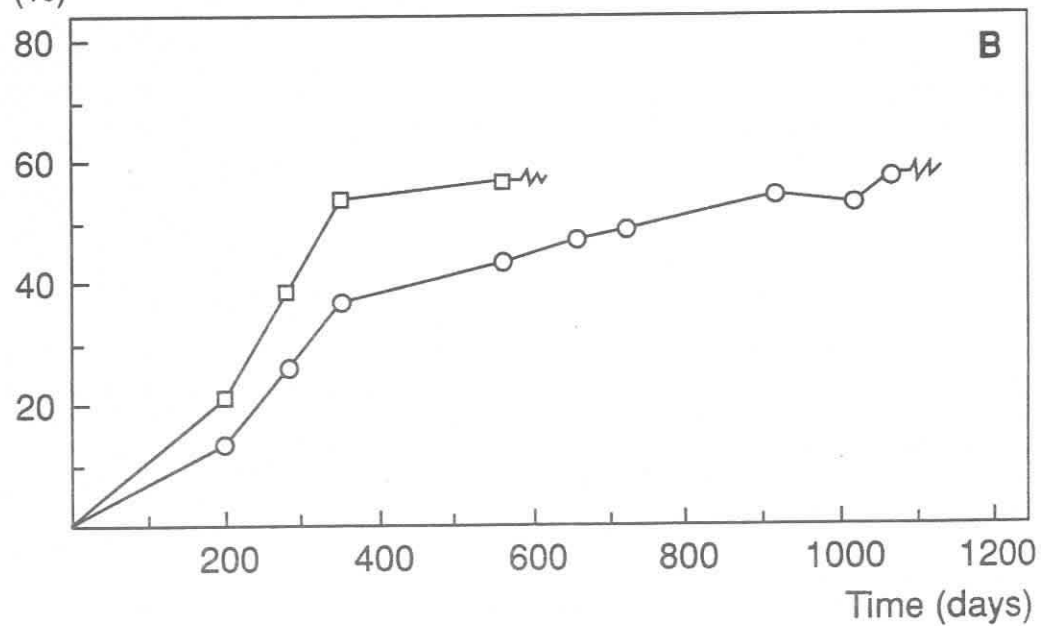


Figure 3. Litter mass loss for brown (o) and green (□) Scots pine needle litter in a control plot (A) and an irrigated plus fertilized plot (B).

References

- Aronsson, A. 1985.** Indications on stress at unbalanced nutrient contents of spruce and pine. *Journal of the Royal Academy of Agriculture and Forestry. Supplement No 17*, 40-51. (In Swedish, English summary)
- Axelsson, B. and Bråkenhielm, S. 1980.** Investigation sites of the Swedish Coniferous Forest Project - Biological and Physiographical features. *Ecological Bulletins (Stockholm)* 32, 25-46.
- Berg, B. 1984.** Decomposition of root litter and some factors regulating the process. Long-term root litter decomposition in a Scots pine forest. *Soil Biology and Biochemistry* 16, 609-617.
- Berg, B. 1986.** Nutrient release from litter and humus in coniferous forest soils - a mini review. *Scandinavian Journal of Forest Research* 1, 359-370.
- Berg, B. and Ågren, G. 1984.** Decomposition of needle litter and its organic-chemical components. Theory and field experiments. Long-term decomposition in a Scots pine forest III. *Canadian Journal of Botany* 62, 2880-2888.
- Berg, B. and Ekbohm, G. 1991.** Litter mass-loss rates and decomposition patterns in some needle and leaf litter types. Long-term decomposition in a Scots pine forest VII. *Canadian Journal of Botany* 69, 1449-1456.
- Berg, B. and Lundmark, J.-E. 1987.** Decomposition of needle litter in lodgepole pine and Scots pine monocultures - a comparison. *Scandinavian Journal of Forest Research* 2, 3-12.
- Berg, B. and Staaf, H. 1980a.** Decomposition rate and chemical changes of Scots pine needle litter. I. Influence of stand age. *Ecological Bulletins (Stockholm)* 32, 363-372.
- Berg, B. and Staaf, H. 1980b.** Decomposition rate and chemical changes in Scots pine needle litter. II. Influence of chemical composition. *Ecological Bulletins (Stockholm)* 32, 373-390.
- Berg, B. and Tamm, C.O. 1991a.** Decomposition and nutrient release of Norway spruce needle litter. I. Organic matter decomposition. *Scandinavian Journal of Forest Research* 6, 305-321.
- Berg, B. and Tamm, C.O. 1991b.** Decomposition and nutrient dynamics of Norway spruce needle litter in a long-term optimum nutrition experiment. Swedish University of Agricultural Sciences. Department of Ecology and Environmental Research. Report No 43.
- Berg, B. and Theander, O. 1984.** The dynamics of some nitrogen fractions in decomposing Scots pine needles. *Pedobiologia* 27, 161-167.
- Berg, B., Wessen, B. and Ekbohm, G. 1982a.** Nitrogen level and lignin decomposition in Scots pine needle litter. *Oikos* 38, 291-296.
- Berg, B., Jansson, P.E. and McClaugherty, C. 1990.** Climatic variability and litter decomposition rates. - European Conference on Landscape - Ecological Impact of Climatic Change. Luntenen, 3-7 Dec 1989. IOS Press, Amsterdam. pp 250 -273.
- Berg, B., Hannus, K., Popoff, T. and Theander, O. 1982b.** Changes in organic-chemical components during decomposition. Long-term decomposition in a Scots pine forest I. *Canadian Journal of Botany* 60, 1310-1319.
- Berg, B., Ewertsson, A., Ferenczi, J., Holm, B., Jansson, P.-E., Koivuhoja, S., Meentemeyer, V., Nyman, P., Staaf, H. and Staaf, I. 1986.** Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites 1st edition. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences. Report No 22, 386 pp.
- Berg, B., Booltink, H.G.W., Breymeyer, A., Ewertsson, A., Gallardo, A., Holm, B., Jansson, P.-E., Johansson, B.-B., Koivuhoja, S., Meentemeyer, V., Nyman, P., Olofsson, J., Pettersson, A.-S., Reurslag, A.-M., Staaf, H., Staaf, I. and Uba, L. 1991.** Data on needle litter decomposition and soil climate as well as site characteristics for some coniferous forest sites. 2nd edition. Department of Ecology and Environmental Research. Swedish University of Agricultural Sciences. Report No 42.
- Bethge, P.O., Rådeström, R. and Theander, O. 1971.** Kvantitativ kolhydratbestämning - en detaljstudie. Comm. from Swedish Forest Product Research Laboratory. 63B. Stockholm (In Swedish).
- Dugger, W.M. 1983.** Boron in plant metabolism. In: Inorganic plant nutrition, vol 15 B. Edited by A.Lückli and R.L. Bielecki. Springer-Verlag, Berlin. pp 626-650.
- Edmonds, R.L. 1980.** Litter decomposition in Douglas fir, red alder, western hemlock, and Pacific silver fir systems in western Washington. *Canadian Journal of Forest Research* 10, 327-337.

- Fogel, R., and Cromack, K. 1977.** Effect of habitat and substrate quality on Douglas fir litter decomposition in Western Oregon. *Canadian Journal of Botany* 55, 1632-1640.
- Hesselman, H. 1937.** Om humustäckets beroende av ålder och sammansättning i den nordiska granskogen av blåbärsrik *Vaccinium* typ och dess inverkan på skogens föryngring och tillväxt. *Meddelanden från Statens Skogsförsöksanstalt* 30, 539-715 (In Swedish, German summary).
- Holmen, H. 1983.** Forest fertilization in Sweden 1983. *Kungl. Skogs- och Lantbruksakademiens Tidskrift* (In Swedish, English summary).
- Ingestad, T. 1967.** Methods for uniform optimum fertilization of forest tree plants. XIV IUFRO Congress Section 22. München. pp 265-269.
- Jansson, P.-E. and Berg, B. 1985.** Temporal variation of litter decomposition in relation to simulated soil climate. Long-term decomposition in a Scots pine forest V. *Canadian Journal of Botany* 63, 1008-1016.
- Kelly, I.M. and Henderson, G.S. 1978.** Effects of nitrogen and phosphorus additions on deciduous litter decomposition. *Soil Science Society of America Journal* 42, 972-976.
- McClagherty, C. and Berg, B. 1987.** Cellulose, lignin, and nitrogen levels as rate-regulating factors in late stages of forest litter decomposition. *Pedobiologia* 30, 101-112.
- Meentemeyer, V. 1978.** Macroclimate and lignin control of litter decomposition rates. *Ecology* 59, 465-472.
- Melin, E. 1928.** Biological decomposition of some types of litter from North American forests. *Ecology* 11, 72-101.
- Miller, H.G. and Miller, J.D. 1976.** Analysis of needle fall as a means of assessing nitrogen status in pine. *Forestry* 49, 57-61.
- Nordén, B. and Berg, B. 1989.** A non-destructive method (solid state ^{13}C -NMR) for determining organic chemical components of decomposing litter. *Soil Biology and Biochemistry* 22, 271-275.
- Pandey, U., and Singh, J.S. 1982.** Leaf-litter decomposition in an oak conifer forest in Himalaya; the effects of climate and chemical composition. *Forestry* 55, 47-60.
- Persson, T., Båth, E., Clarholm, M., Lundkvist, H., Söderström, B. and Sohlenius, B. 1980.** Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a Scots pine forest. *Ecological Bulletins (Stockholm)* 32, 419-462.
- Sirén, G. 1955.** The development of spruce forest on raw humus sites in northern Finland and its ecology. *Acta Forestalia Fennica* No 62.
- Söderström, B., Båth, E. and Lundgren, B. 1983.** Decrease in soil microbial activity and biomasses according to nitrogen amendments. *Canadian Journal of Microbiology* 29, 1500-1506.
- Staaf, H. and Berg, B. 1989.** Fömanedbrytning som variabel för miljö kvalitetskontroll i terrester miljö. I. Substraturval och inledande studier. *Statens Naturvårdsverk (Stockholm) PM No 3591*, 52 pp (In Swedish, English summary).
- Svensson, G. and Anfält, T. 1982.** Rapid determination of ammonia in whole blood and plasma using flow injection analysis. *Clinica Chimica Acta* 119, 7-14.
- Tamm, C.O. and Carbonnier, C. 1961.** Plant nutrients and forest yields. *Kungl. Skogs- och Lantbruksakademiens Tidskrift*. 100, 96-124.
- Tamm, C.O., Aronsson, A. and Burgtorf, H. 1974.** A brief description of an experiment in a young stand of Norway spruce. *Inst. f. växtekologi & marklära, rapport nr 17*, 34 pp. Uppsala: Lantbruksuniversitet. (In Swedish, English summary).
- Van Cleve, K. 1974.** Organic matter quality in relation to decomposition. In: *Soil Organisms and Decomposition in Tundra*, pp 311-324. (Edited by Holding, A.J., Heal, O.W., MacLean, S.F., and Flanagan, P.W.) *Tundra Biome Steering Committee, Stockholm*.
- Vedin, H. 1973.** Medeltemperaturer 1931-1960. Referensnormaler. Reviderad upplaga, Maj 1973. SMHI Rapporter. Norrköping (In Swedish).

Table 1. Some chemical properties of Scots pine needle litter sampled at a fertilization-irrigation experiment at Jädraås Experimental Station. Average values are given with standard deviation within parentheses. C stands for control plot; I for irrigated plot; F for fertilized plot and IF for irrigated plus fertilized plot. n gives the number of experimental plots sampled

Sampling year	n	Concentration of chemical component (%)			
		Type of plot			
		C	F	I	IF
Nitrogen					
1976	1	0.36	0.41	0.38	0.44
1977	1	0.36	0.41	0.36	0.46
1982	1	0.39	0.48	0.36	0.39
1983	4	0.36	0.38	0.34	0.44
1984	4	0.33	0.41	0.35	0.45
Mean	5	0.36 (0.019)	0.42 (0.033)	0.36 (0.013)	0.44 (0.024)
Water solubles					
1982	1	21.3	13.8	13.1	17.0
1983	4	21.5 (1.19)	21.5 (0.43)	11.5 (0.74)	9.3 (0.91)
1984	4	10.5 (1.16)	8.5 (0.50)	9.6 (0.84)	8.1 (0.13)
Mean	3	17.8 (5.14)	14.6 (5.34)	11.4 (1.43)	11.5 (3.94)
Ethanol solubles					
1982	1	9.4	10.6	11.7	9.4
1983	4	11.1 (0.63)	9.7 (0.39)	11.9 (0.67)	10.4 (1.07)
1984	4	12.7 (0.39)	12.6 (0.55)	11.8 (0.48)	10.5 (0.60)
Mean	3	11.1	11.0	11.8	10.1
Lignin					
1982	1	23.1	25.2	25.9	23.7
1983	4	21.8 (0.21)	20.2 (0.30)	26.7 (0.13)	26.5 (0.72)
1984	4	26.6 (0.74)	26.2 (0.39)	27.1 (0.38)	26.2 (0.70)
Mean	3	23.8 (2.03)	23.9 (2.62)	26.6 (0.50)	25.5 (1.26)

Table 2. Concentrations of some chemical components in Scots pine needle litter at the optimum nutrition experiment at site Norrliden. The sampling was made in September of the years 1983 and 1984. Standard deviation within parantheses.

Type of plot and sampling year	Concentration (mg g ⁻¹)			P	N	n	
	Water solubles	Ethanol solubles	lignin				
1983							
Control	132	(15.8)	118 (6.4)	262 (13.4)	3.8 (0.2)	0.25 (0.02)	12
N1	122	(10.9)	113 (5.0)	268 (7.4)	n.d.	n.d.	6
N2	129	(6.0)	119 (9.2)	262 (10.0)	n.d.	n.d.	7
N3	127	(15.8)	122 (11.4)	262 (14.2)	8.3 (0.6)	0.26 (0.02)	6
P2K2	126	(9.4)	119 (7.3)	263 (6.8)	n.d.	n.d.	3
Lime	132	(20.3)	120 (10.3)	258 (22.4)	3.8 (0.0)	0.25 (0.03)	3
1984							
Control	97	(3.6)	110 (3.3)	273 (2.4)	n.d.	n.d.	6
N3	95	(7.2)	117 (7.9)	271 (6.9)	6.1 (0.85)	n.d.	6

Table 3. Litter mass loss in the first incubation year in plots of four different treatments in an irrigation- fertilization experiment at Jädraås Experimental Station. Control plot (C); Irrigation (I); Fertilization (F); Irrigation+ Fertilization (IF). Standard error within parantheses. Those values within each incubation period that are significantly different are indicated by the same letter. After 850522 the experiment in the I+F plot was terminated.

Litter mass loss (%) and plot				
Incubation period	C	I	F	IF
821102-831026	21.6 (0.87)	34.2 (0.81)	29.5 (0.86)	36.8 (0.76)
831026-841030	26.8 (0.73)	29.9 (1.45)	29.5 (0.74)	43.9 (1.18)
840523-850522	31.1 (0.63)	36.7 (0.96)	33.1 (0.80)	47.6 (0.79)
841030-851015	23.2 (0.63)	28.2 (1.06)	25.5 (0.70)	n.d.
850522-860524	n.d.	31.4 (0.98)	n.d.	n.d.
851017-861020	25.4 (0.50)	27.7 (1.00)	25.4 (0.74)	n.d.
861020-871021	32.0 (1.08)	25.8 (0.88)	28.3 (0.53)	n.d.
Mean value	26.7	30.6	28.6	42.8

Table 4. First-year mass loss of a unified preparation of Scots pine needle litter in three plots at the site Norrleden. One plot was not fertilized (control) one moderately fertilized (N1P2) and one heavily fertilized with N and P (N2P2). Standard error within parantheses. The value for standard error presented are for the variation among the one-year values. Those values within each incubation period that are significantly different are indicated by the same letter.

Time period	Mass loss (%)					
	control plot		N1P2 plot		N2P2 plot	
830607-840605	27.9 ^a	(0.99)	27.4 ^b	(0.96)	31.5 ^{a,b}	(0.98)
830908-840911	29.3 ^a	(0.76)	-		33.9 ^a	(0.78)
831020-841020	28.4 ^{a,b}	(0.67)	31.6 ^b	(1.32)	31.2 ^a	(0.75)
840605-8506011	24.5 ^{a,b}	(0.95)	28.4 ^b	(1.24)	30.0 ^a	(1.29)
840911-850911	26.3 ^{a,b}	(0.73)	30.6 ^b		30.5 ^a	(0.62)
850611-860611	22.5 ^a	(0.65)	-		26.2 ^a	(0.82)
Mean value	26.5 ^a		29.5		30.55 ^a	
SD	2.36		1.68		2.30	

Appendix 1. Fertilizer regimes for the plots used in the optimum nutrition experiment Norrleden. There was no addition to the control plot.

Year	Type of plot and fertilizer							
	N3	N2	N1	N2P2		N1P2		P2
				N	P	N	P	P
1971	180	120	60	120	40	60	40	40
1972	180	120	60	120	-	60	-	-
1973	180	120	60	120	-	60	-	-
1974	120	80	40	80	40	40	40	40
1975	120	80	40	80	-	40	-	-
1976	120	80	40	80	-	40	-	-
1977	120	80	40	80	40	40	40	40
1978	120	80	40	80	-	40	-	-
1979	120	80	40	80	-	40	-	-
1980	120	80	40	80	40	40	40	40
1981	120	80	40	80	-	40	-	-
1982	120	80	40	80	-	40	-	-
1983	120	80	40	80	40	40	40	40
1984	120	80	40	80	-	40	-	-
1985	120	80	40	80	-	40	-	-
1986	120	80	40	80	40	40	40	40

Appendix 2. Fertilization and irrigation regimes for experimental plots with Scots pine stands. F stands for fertilized plot and IF for irrigated plus fertilized plot.

Year	Period (day,month)	Total water (mm in period) precip. irrigat.		Sum water tot in per day period		In I F	Fertilizers (g m ⁻²) In F			
		(mm)	(mm)				N ¹	N	P	K
1974	1207-1909	100	100	200	2.90	7		8	3	6
1975	2305-1209	180	300	480	4.25	10		8	0	0
1976	2005-1809	250	300	550	4.51	15		8	0	0
1977	1605-3008	240	250	490	4.58	15		8	3	6
1978	2305-1209	320	220	540	4.78	20		8	0	0 ²
1979	2805-1109	290	230	520	4.86	20		8	0	0
1980	2705-0509	250	160	410	4.02	20		8	3	6 ²
1981	0106-1109	280	165	455	4.42	10		5	0	0
1982	2905-0309	180	215	395	4.16	10		5	0	0
1983	2405-0309	150	272	422	4.10	10		5	3	0
1984	2205-0509	300	245	545	5.10	10		5	0	6
1985	0306-2708	250	190	440	5.06	10		5	0	0
1986	0906-2208	260	165	425	5.51	5		5	3	6
1987	0206-3008	265	172	437	4.90	5		5	0	0 ²
1988	1006-0109	280	180	460	5.48	3		3	0	0

1. All other essential nutrients were also added according to Ingestad (1967)

2. In 1978, 1980, and 1987 the F-treatment was, in addition, fertilized with 0.25 g B m⁻² yr⁻¹.